

The Cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent

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Synopsis

An account is given of some fifty articulated specimens of *Cephalaspis* discovered in the mid 1930s by W. N. Croft in a stream section near Abergavenny. All are small animals and are mostly referable to *C. cradleyensis* Stensiö, but three new species *C. cwmmillensis*, *C. abergavenniensis* and *C. (Cwmaspis) billcrofti* subgen. et sp. nov. are also represented.

The development and means of distribution of cephalaspids are discussed.

Introduction

An interesting discovery was made by W. N. Croft in the Dittonian (Lower Devonian) of the Anglo-Welsh area some years ago in a stream section in a small tributary of the River Gavenny at Cwm Mill near Mardy, about one mile (1.6 km) north-east of Abergavenny (National Grid ref. SO 311156). Croft in his original field notes records the locality as lying '¾ mile NNE of Asylum, Abergavenny'.¹ Like virtually all the sections and pits in the region that formerly yielded good cephalaspid material the Cwm Mill locality has now been worked out. Here a thin bed of grey-green siltstone, apparently not more than 2 or 3 inches (c. 65 mm) thick, yielded a quantity of articulated specimens of small *Cephalaspis*. Some fifty specimens were collected and doubtless all, or nearly all, must have been complete when first buried, but they were massed together and flattened, lying top-side up, on their backs, even occasionally on their sides, all close together and very often on top of one another. This, combined with the softness of both matrix and specimens, made collecting very difficult and the results were often rather disappointing.

Nevertheless, the collection is of much interest, for articulated specimens from Dittonian strata of the Anglo-Welsh region are extremely rare – Stensiö (1932) recorded only three specimens with part of the body attached – and at undescribed localities only Wayne Herbert, 10½ miles (17 km) away, has produced articulated cephalaspids in a much more diversified fauna (Miles 1973), while a single complete specimen was found in a nodule in a stone-breaker's pile just below Castle Mattock, some seven miles (11.25 km) north of Cwm Mill.

The Cwm Mill section has already been noticed in literature (White 1950: 56; Allen & Tarlo 1963: 145), and although the fauna has never before been described, the cyclothem of which it forms part has been described in some detail and illustrated by Allen (1964: 184–6, fig. 11). Unfortunately, the precise relationship of the Cwm Mill section to the levels of the principal quarries that have yielded the bulk of useful material during the last half century is not known. While those quarries lie in a stable block dipping gently to the south-east and can be related to the 'Psammosteus Limestone' (P.L.), Cwm Mill is in a much less stable area where there is no sign of the P.L., but Allen in his description of the cyclothem states that it 'lies about the middle of the Dittonian stage'.

¹The field notebooks of W. N. Croft (1915–1953) are housed in the Department of Palaeontology, British Museum (Natural History).

It may be convenient at this point to list the principal quarries of the area, with the attendant form of *Pteraspis* (White 1935; 1950: 58 footnote): all are now out of use and largely overgrown:

WERN (or GWYN) GENNI. 650 feet (200 m) above P.L. 6 miles (9.6 km) NW of Wayne Herbert. With *Pteraspis stensioi*.

POOL QUARRY. 350 feet (110 m) above P.L. 3½ miles (5.6 km) SSE of Wayne Herbert. With typical *P. crouchi* and *P. rostrata* var. *waynensis*.

CASTLE MATTOCK (CLODOCK). 240 feet (75 m) above P.L. 3½ miles (5.6 km) south of Wayne Herbert. With *P. jackana* and *P. crouchi* var. *mattockensis*.

WAYNE HERBERT. 220 feet (67 m) above P.L. 11½ miles (18.5 km) NNE of Abergavenny. With *P. rostrata* var. *waynensis*, *P. rostrata* var. *virgoi* and *P. ?jackana* above siltstone lenticle and *P. rostrata* var. *toombsi* in it.

CWM MILL. 'About the middle of the Dittonian stage'. 1¼ miles (2 km) NE of Abergavenny and 10½ miles (17 km) SSW of Wayne Herbert. With *P. ?crouchi*.

The specimens used in the compilation of this paper belong to the collections of the British Museum (Natural History), London and are referred to by register number with or without the prefix P.

The Cwm Mill Fauna

This was a very restricted exposure for the fossil vertebrates; apart from scattered fragments, they occur 'from a distinct horizon' (Allen 1964: 185, fig. 11) over a distance of not more than a foot or two (less than 1 m). Curiously enough Croft in his field notes made very little reference to the discovery of this remarkable assemblage of ostracoderms. Under the heading '*Cwm Mill – Cephalaspis* Loc. (244)' he gives a section 26 inches (0.66 m) in height in which is shown a bed 2–3 inches (c. 65 mm) thick simply labelled 'Pt. (rare) above. Ceph. below': yet from this small exposure an unprecedented number of specimens of *Cephalaspis*, originally complete, were extracted from a single layer, a grey-green siltstone, which seems to have been lenticular.

All the specimens except three seem to belong to a single species, *Cephalaspis cradleyensis* Stensiö, while each of the remainder belongs to a different undescribed species. Outside the siltstone lenticle a darker, harder bed yielded a few fragments of still other species of the genus, in addition to pieces of cephalic discs of *C. cradleyensis*.

The fauna of the siltstone lenticle

Family CEPHALASPIDAE Agassiz, 1843

Genus CEPHALASPIS Agassiz, 1835

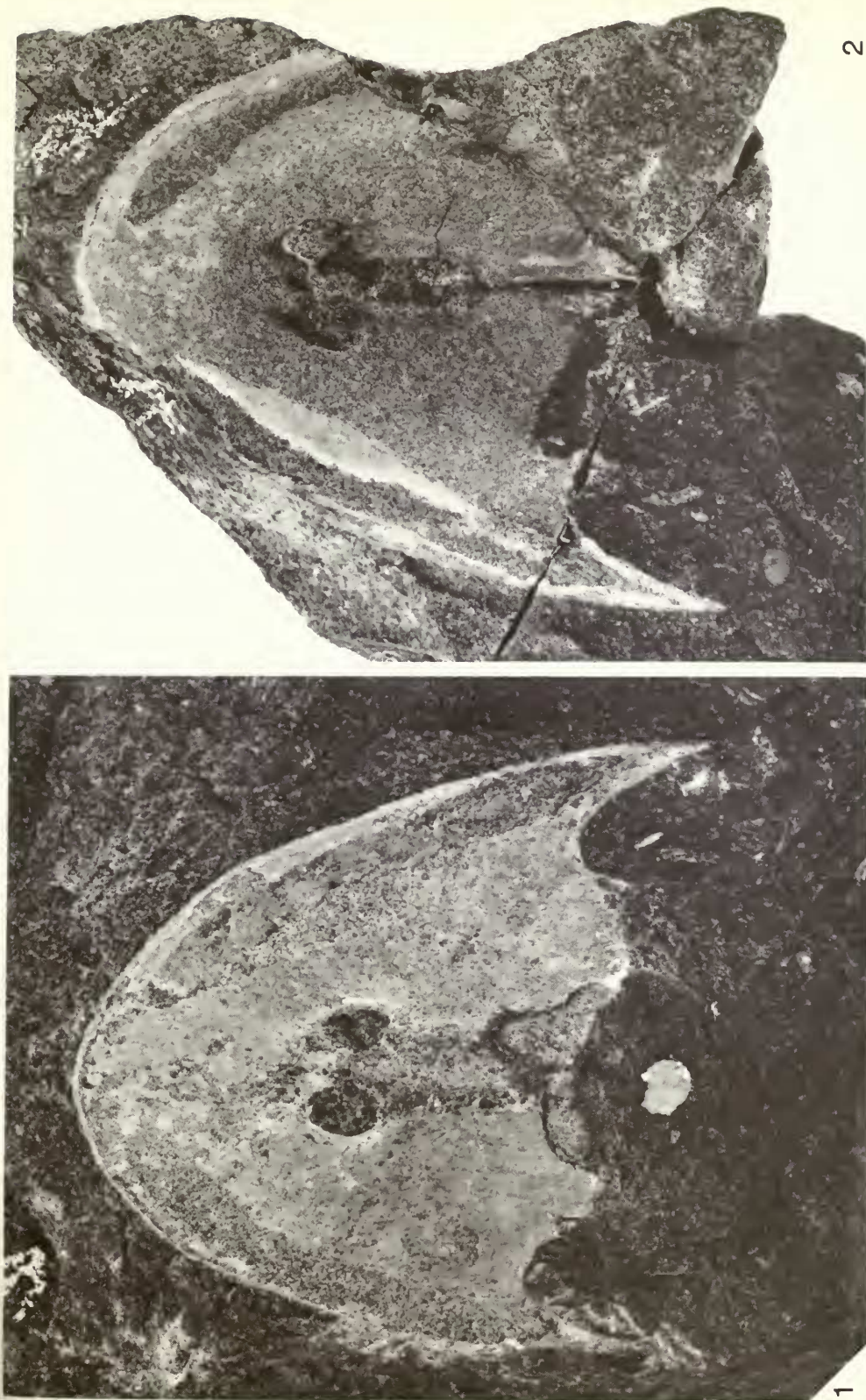
Cephalaspis cradleyensis Stensiö

Figs 1–11

1932 *Cephalaspis cradleyensis* Stensiö: 130, text-fig. 44; pl. 15, fig. 6.

1952 *Cephalaspis cradleyensis* Stensiö; Wängsjö: 255, text-fig. 24; pl. 2.

DIAGNOSIS (emended). A small species of *Cephalaspis* with total length 100–120 mm. Cephalic shield about 40 mm long and approximately 40 mm in maximum breadth measured across the tips of the cornua. Lateral margins of shield gently convex, narrowing rather rapidly towards a rounded front without rostral angle. Cornua directed slightly laterally, short, their length scarcely exceeding one quarter of distance between tips and median point of rostral margin; inner margins without denticles. Pectoral sinus rather narrow and shallow; interzonal part broad and short with low but well-defined median crest projecting a little to form a very short posterior angle. Orbital openings somewhat oval and situated rather nearer front than back of shield. Dorsal sensory field long and narrow, about three and half times as long as maximum breadth, and pointed behind. Lateral sensory fields reaching a short distance externally onto surface of



Figs 1-2 *Cephalaspis cradleyensis* Stensiö. Fig. 1, imperfect cephalic shield, the holotype (P.5375), $\times 2.4$. Fig. 2, counterpart of same (P.16960), $\times 2.4$.

cornua. Surface of cephalic shield smooth except for fine denticles around orbits, and with up to twenty rows of fine pits parallel with margins under brim. About 22 rows of scales in front of dorsal fin with at least six ridge-scales.

HOLOTYPE. Cephalic shield P.5375 (Fig. 1); counterpart P.16960 (Fig. 2); Lower Old Red Sandstone, Cradley, Herefordshire.

MATERIAL. Some 42 individuals on 18 blocks, all from Middle Dittonian of Cwm Mill. In some instances a single specimen block contains more than one species and for this reason individuals are separately numbered. The following specimens are from the principal siltstone band: P.22973, P.22974a, b, P.22990–2, P.22993a, b, P.22994, P.22998a, b, P.22999a, b, P.23000a, b, P.23001a, b, P.23002a, b, P.23003a, b, P.23004a, b, P.23005a, b, P.23008–9 (part and counterpart), P.23010a, b, P.23013, P.60867–8 (part and counterpart), P.60869a, b, P.60870–4, P.60875a, b, P.61033a, b, P.61035a, b, P.61036a, b, P.61037–42, P.61043a, b, P.61044a, b, P.61045–6, P.61047a, b. The remainder are from the hard darker bed: P.23006–7 (part and counterpart), P.25100, P.25178–9 (part and counterpart).

Cephalaspis cradleyensis is noteworthy in that it is the only species of the genus so far recorded as being common to the Anglo-Welsh area and Spitsbergen. The original description was based on a single specimen without counterpart from Cradley, Hereford and Worcester, consisting of a small, imperfect and somewhat distorted cephalic shield which certainly did not allow more than a very restricted diagnosis of the species (Fig. 1). This specimen was purchased by the Museum with the H. B. Hill Collection in 1887 but is not recorded by Woodward (1891), possibly on account of its relative insignificance. The counterpart, recorded and figured for the first time here (Fig. 2), was discovered in 1934 in the Museum at Bootle in Lancashire and was then generously presented to the British Museum (Natural History) by the Committee of that Museum. The specimen had been bought originally from the well-known dealer in fossils, J. R. Gregory of London, as an example of *Cephalaspis lyelli*.

DESCRIPTION. Most of the specimens from Cwm Mill are in some respects rather disappointing in spite of their original completeness. The siltstone matrix and the armour of the animals are relatively soft and are often not easy to develop profitably with either tools or acid, and all too often magnification does little to clarify details. All from the siltstone are flattened.

The holotype and its newly figured counterpart have the great advantage of being three-dimensional and show a depth at the back of the skull of 12 mm without the crest and, with the Cwm Mill specimens, it is possible to correct for distortion in regard to the size and form of the cornua, so that a reasonable restoration of the cephalic shield may be made (Fig. 6, p. 155).

The finest of the Cwm Mill slabs (with its counterpart) is undoubtedly that shown in Fig. 3, for on its surface are the remains of at least seven specimens, four of which, labelled in the figure as B (P.22999a), C (P.61043a), D (P.61044a) and E (P.61045), are very nearly complete and show the squamation of the body reasonably well; the fins and tail are, however, poorly preserved. All the specimens except D lie in the usual dorso-ventral position, and as the shields are almost completely flattened the front margins appear entirely rounded, almost semicircular, whereas specimen D lies, most exceptionally, on its side with the cephalic shield almost in lateral profile. A second specimen (P.23003a; Fig. 7, p. 157) is in a similar position.

The total length of a complete specimen with tail would be about 120 mm, with the median length of the head, the body from head to base of tail, and the tail itself all very nearly equal, about 40 mm apiece; and 40 mm is the average maximum breadth, measured across the tips of the cornua, in a flattened cephalic shield. There is one specimen that shows nearly the whole length of the fish, only lacking the tip of its tail (P.23000a, b) and this has approximately the proportions given.

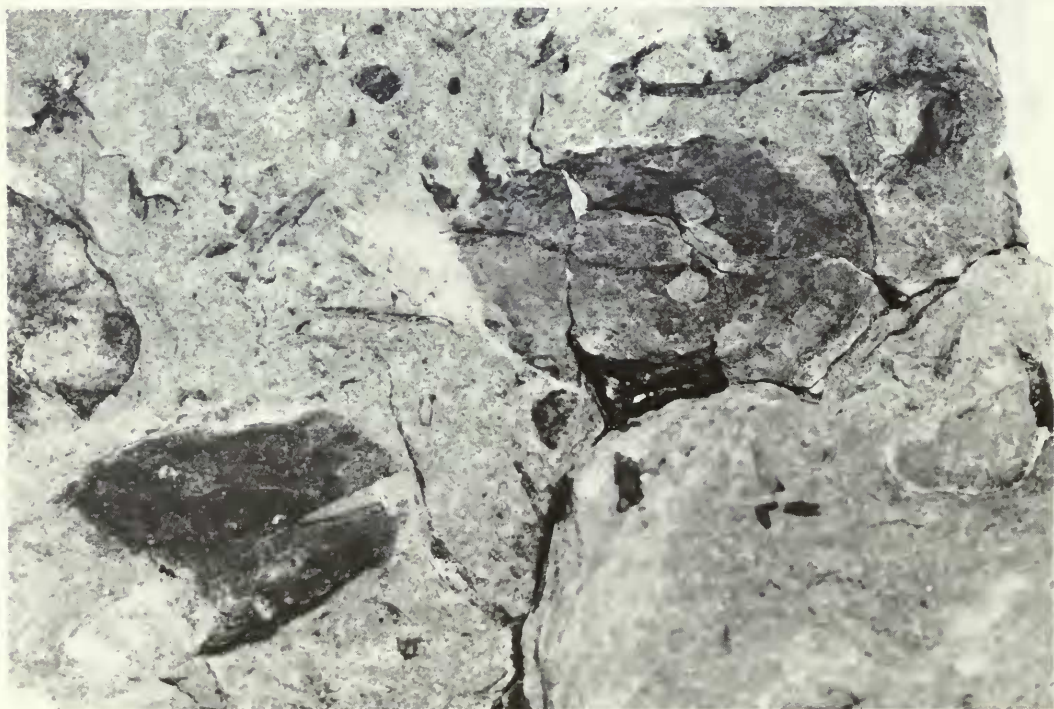
A most typical cephalic shield is P.23008–9 and to this in the counterpart is attached part of the body with the impression of some of the left paddle. The shield is less crushed than many of the other specimens and gives a more accurate impression of the shape. The polygons formed by the inter-areal canals of the mucous canal system are as a rule not visible as the superficial layer of the exoskeleton is continuous, but they do appear occasionally, as in the interzonal part of this



Fig. 3 *Cephalaspis cradleyensis* Stensiö. Siltstone block showing remains of four nearly complete individuals, lettered B (P.22999a), C (P.61043a), D (P.61044a) and E (P.61045). $\times 1.3$.



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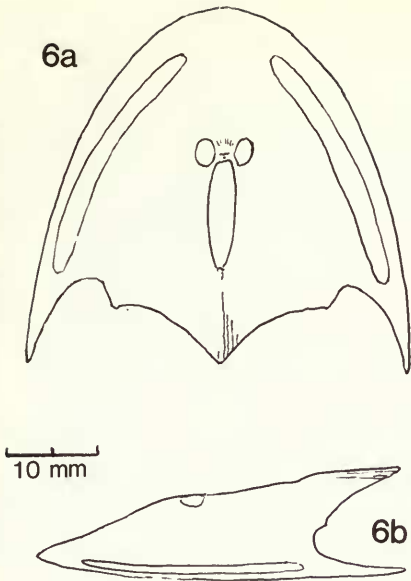


Fig. 6 *Cephalaspis cradleyensis* Stensiö. Restoration of cephalic shield based on holotype (P.5375) and its counterpart (P.16960), and on P.25178–9; in dorsal view (a) and left lateral view (b).

specimen, not naturally but due to the cracking of the convex surface along such lines of weakness under pressure. There is a low but very definite ridge or spine medially on the short but wide interzonal part, with correspondingly narrow and shallow pectoral sinuses.

The best example of the median area of a dorsal shield of *C. cradleyensis* is shown on a piece of the succeeding darker shaly bed (P.25178–9; Fig. 5). The specimen, like the original shield from Cradley, is almost uncrushed, although both sides have been broken away. The median length of the shield is 38 mm; the pineal plate is 16 mm from the rounded anterior margin, while the orbits are each 14 mm away from its centre point. They are oval and measure 4 mm long by 3 mm at their widest. The dorsal sensory field is long and narrow, measuring 12×5 mm, and is pointed behind. The lateral sensory fields are 3.5 mm wide in front and are there separated by 6 mm. It is partly on this specimen that the restoration in Fig. 6 is based.

The external surface of the visceral exoskeleton is very well seen in impression in P.60868 (Fig. 10, p. 161): there is the same cover of small scales, numerous and irregular in shape, as Stensiö (1932: 43, fig. 8) illustrated in *Hemicyclaspis*, and there is a similar wide and narrow mouth. In P.23010 (Fig. 9, p. 159), in addition to mouth and scales, there are impressions of at least eight box-like branchial pouches on each side. Curiously enough, each of these two specimens has superimposed on the details of the ventral surface clear impressions of the central features of the dorsal exoskeleton; the orbits, the pineal plate, the circumnasal fossa and part of the dorsal sensory field (Fig. 10)! Branchial pouches, ventral scales and part of the mouth are also to be seen in P. 22993a.

Ornamentation is absent on the upper surface of the cephalic shield except for small areas of minute tubercles around the orbits and the circumnasal fossa. Under the brim of the shield there

Figs 4–5 *Cephalaspis cradleyensis* Stensiö. Fig. 4, part of a siltstone block: above, in faint outline a whole specimen, probably a juvenile with incompletely developed armour (P.23005a); below, a normally developed cephalic shield (P.23004a); $\times 1.8$. Fig. 5, block from darker rock showing, at top right, an imperfect but well-preserved cephalic shield of *C. cradleyensis* (P.25178); also dorsal and ventral discs of *Pteraspis* (*Belgicaspis*) *crouchi* (P.61150), either from a small variety or young specimens, with fragments of plants; $\times 1.6$.

are many rows of minute pittings running parallel with the margin (P.60868; Fig. 10). On the body-scales there are numerous short grooves parallel with the length that vary greatly in definition.

The orbits were said by Stensiö to be 'rather or fairly large', but it must be remembered that the eye-socket is a truncated cone so that the inner aperture in the basal layer, which Stensiö was in fact seeing in the type-specimen, can be, and indeed was, substantially larger than the external opening seen in the counterpart, which was rather on the small side (cf. Figs 1 and 2). They are oval, those in P. 23008-9 measuring approximately 4 mm long and 3 mm wide in a shield measuring 40 mm along the mid-line.

A similar caution should be observed in regard to the length of the lateral sensory fields and the extent to which they are supposed to run onto the bases of the cornua, since their cavity extends beyond the tessellated upper surface; if that is removed the field may appear to go further than it does in fact. In *C. cradleyensis* the lateral sensory fields are narrow and long and do continue on to the short cornua.

The dorsal sensory field is also long and narrow, and in P. 23010b it measures 11 mm in length and 3.5 mm at its widest.

The arrangement of the squamation is much the same as in *C. lyelli* (White 1958a), except that the main lateral row appears to be rather deeper and the scales are much subdivided immediately behind the head-shield. The dorsal median scale marking the position of the lost anterior dorsal fin is relatively insignificant. There are approximately 22 scale-rows to the level of the remaining dorsal fin.

The finest tail in the collection is P.22974a, b (Fig. 8, A). It is preserved in a completely lateral position. Unfortunately all the cephalic shield is lost so that the specific identity of the specimen is not absolutely sure, but although the body is a shade larger than in other specimens, it does show similar features. The cut-water scales of the dorsal fin are large and six or seven of them are very well seen, and there are at least 32 ridge-scales along the upper margin of the tail-fin. Between the latter and the main squamation of the tail and again between the main squamation and the ventral fin-rays there are single rows of minute longitudinal scales. There are more than fifty main rows of scales on the tail. The 'fin-rays' are formed of very small scales in rows that bifurcate at least twice to form the fringe of the tail-fin.

Remains of the 'horizontal antero-ventral lobes of the tail' (Heintz 1939: 112) or 'ventral axis of caudal fin' (*vhp.* in Stensiö 1932: pl. 34) may be seen in this and other specimens but nowhere to advantage.

The pectoral fins or paddles are represented in several specimens, usually by impressions of the basal part, but in P.23002a there is a faint but complete impression of the left fin (Fig. 7, top). It is 13 mm in length with a maximum breadth of 6 mm. The shape is rather leaflike with a gently convex outer margin and a slightly sinuous inner margin, forming a rather broad terminal point. The scales on the limb are as usual largest at the base, diminishing in size distally and marginally. This specimen is of the usual size, with the cephalic shield 40 mm in median length.

The specimens in the darker bed (P.23006-7, P.25100 and P.25178-9) are all imperfect isolated cephalic shields, associated with broken dorsal and ventral discs of *Pteraspis* cf. *crouchi*. As noted before, in spite of their imperfections, the specimens from this bed are much better preserved in detail and less crushed than the more complete specimens from the main bed.

Uncrushed shields of *Cephalaspis cradleyensis* are very simple in form and at a glance not unlike small editions of the genotype, *C. lyelli*, but even so there are no species recorded from the Anglo-Welsh or Spitsbergen areas with which this species may be confused except that represented by the unique specimen from the latter province which Wängsjö (1952: 255, fig. 24; pl. 2) placed in *C. cradleyensis* itself. However, there do seem to be differences between that specimen and those from the Anglo-Welsh area. The latter do not show a rostral angle nor denticles along the inner margins of the cornua (Figs 1-2), as Stensiö averred in his original description of the species (1932: 130, fig. 44; pl.15, fig. 6). These features do not appear to be very obvious in either of the figures in Wängsjö's plate. It is probably safer then to label the rather poorly preserved, unique specimen from Spitsbergen simply as '*Cephalaspis* cf. *cradleyensis*' and to await further discoveries.



Fig. 7 *Cephalaspis cradleyensis* Stensiö. Siltstone block with the remains of four specimens, that on the left (P.23003a) lying on its side. Other specimens visible are P.61035a and P.23002a; $\times 1.9$.

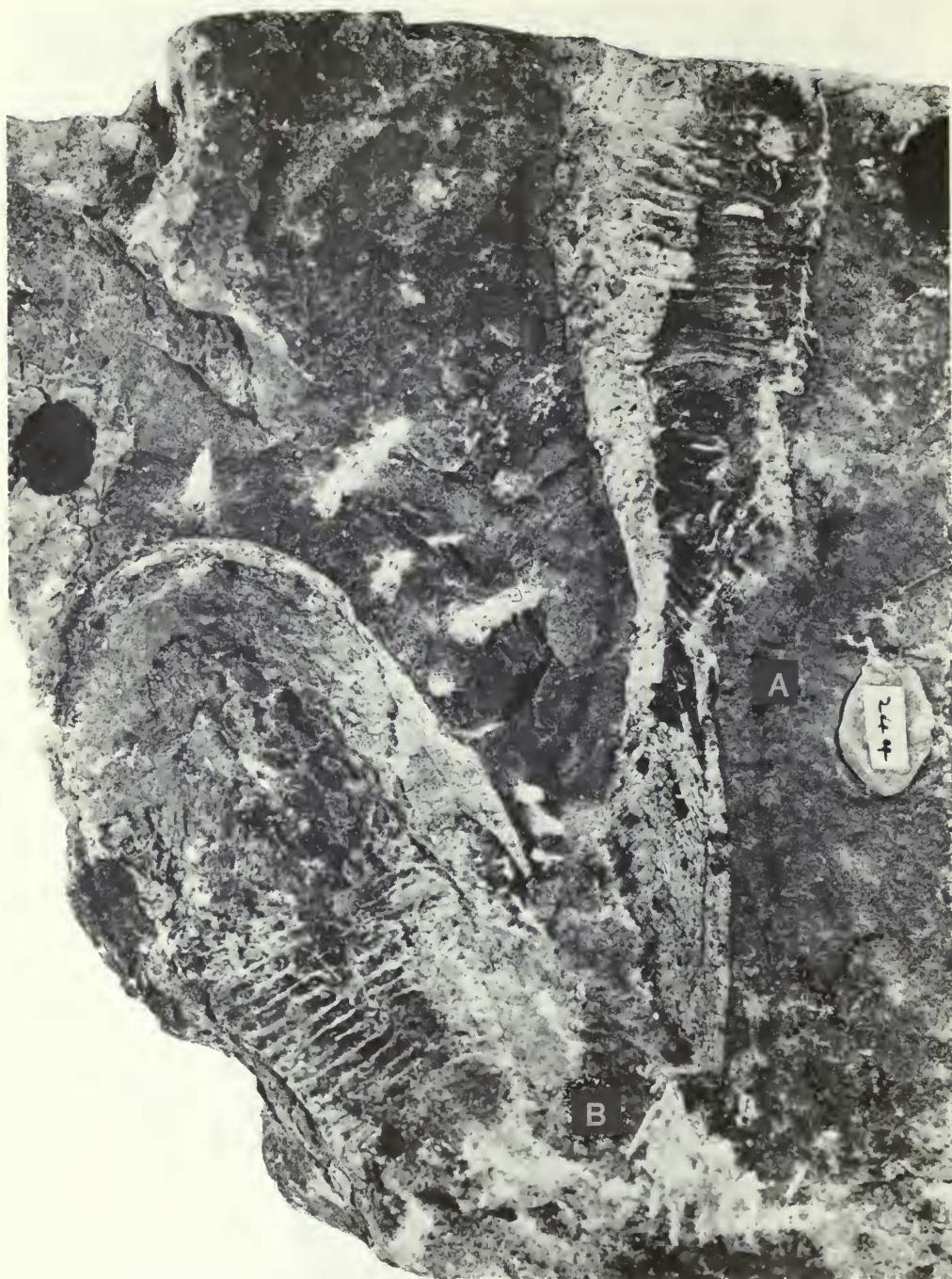


Fig. 8 *Cephalaspis cradleyensis* Stensiö. Siltstone block showing a complete body and tail lying on one side, A (P. 22974a); and a much flattened cephalic shield with part of the body, B (P. 22973); $\times 1.7$.



Fig. 9 Siltstone block with two specimens of *Cephalaspis*. The larger specimen (P.23010a) is an example of *C. cradleyensis* and shows the impression of most of the lower surface of the body and almost all the undersurface of the cephalic shield with mouth, scales and branchial pouches on each side. The smaller specimen at the top (P.23011a) is the **holotype** of *C. cwmmlensis* sp. nov. which shows the inner impression of the head and the ventral impression of the right cornu. $\times 2.1$.

Cephalaspis cwmmillensis sp. nov.

Figs 9, 12–14

DIAGNOSIS. A species of *Cephalaspis* of very small size with maximum breadth of cephalic shield, at base of cornua, about 1.25 times as great as length of shield in median line. Shield narrows evenly in front without rostral angle and with sides forming a continuous curve with cornua. Cornua broad at base but narrowing rapidly to a fine point distally and curving gently inwards to a level a little behind that of posterior interzonal angle. The distance from the cornual tips to the centre of rostral margin about $3\frac{1}{3}$ times as long as the length of the cornua. Inner margins of cornua without denticles. Pectoral sinuses narrow and deep. Interzonal part short and broad, its breadth between posterolateral angles being about half maximum breadth of shield, with low median ridge. Posterior angle of interzonal part approximately a right angle, reaching well behind posterolateral angles. Dorsal sensory field narrow, nearly four times as long as broad and blunt behind. Lateral sensory fields narrow and short, not reaching onto cornua. Orbital openings relatively large, oval in shape, lying considerably nearer pectoral sinuses than rostral margin of shield. Small independent pineal plate present. Exoskeleton ornamented with numerous minute thorn-like denticles.

HOLOTYPE. Imperfect cephalic shield in counterpart P.23011a, b: Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

DESCRIPTION. This shield is reasonably well preserved, its deficiencies being largely due to difficulties in collecting. Originally doubtless much of the body was attached, but as it is, the left cornual region and the whole of the body has been lost save for the impressions of a few fragments of body-scales and of the base of the right paddle on the counterpart. The right cornua lay under the cephalic rim of a head shield of a specimen of *C. cradleyensis* described above (Fig. 9). The specimen of *C. cwmmillensis* is one of the few specimens from this locality that show fair impressions of any of the vessels of the head (Fig. 12).

The median length of the shield is approximately 28 mm and the estimated maximum breadth, across the base of the cornua, is 34 mm. The breadth of the interzonal part between the posterolateral angles was about 16 mm; the length of the surviving cornu is 10 mm and the distance of its tip from the centre of the front margin of the shield is 34 mm; the distance of the pineal foramen from the posterior tip of the shield is 14 mm and about the same from the rostral end, so that the oval orbits were approximately at the middle of the length of the shield but very much nearer to the pectoral sinuses than to the rostral margin. They measure 3×2.25 mm.

The shield is not especially broad but a notable feature is the almost even, continuous curve of the sides and cornu, and although the anterior margin does narrow rather quickly, there is certainly no rostral angle and the inner margin of the broad-based but sharply pointed cornu is smooth. There is some evidence that the interzonal part bore a low median ridge.

The dorsal sensory field is moderately long but almost evenly narrow, and truncated at the posterior end. It measures 2.5×8 mm and is about 7 mm from the posterior point of the interzonal aprt. The lateral sensory fields are also narrow and appear to have been unusually short, stopping some little distance from the base of the cornua.

The exoskeleton is represented by the impression of the external surface only, and this shows that the upper surface was covered with very small thorn-like denticles, while under the brim there were numerous rows of interrupted fine ridges parallel with the outer margin of the shield. The mucous canal system was apparently entirely enclosed in the exoskeleton.

The internal cast shows the impressions of a number of features rarely seen in this fauna, such

Fig. 10 Impression of cephalic shield of *C. cradleyensis* Stensiö showing decoration of the submarginal rim and the ventral scales of the anterior half; and also impressions of the eyes, the circumnasal fossa, the pineal plate and the anterior end of the median sensory field (P.60868). $\times 3.1$.

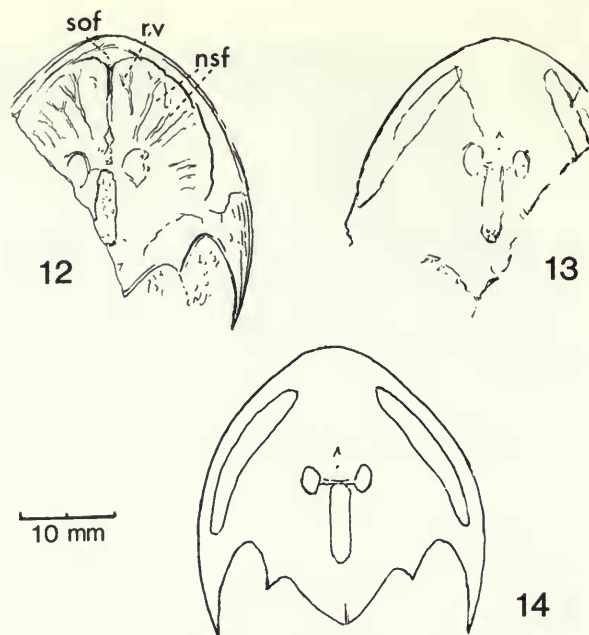
Fig. 11 Part of siltstone slab with **holotype** of *Cephalaspis abergavenniensis* sp. nov. (P.61034b). $\times 2.1$.

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Figs 12-14 *Cephalaspis cwmmillensis* sp. nov. Fig. 12. Dorsal view of holotype (P. 23011a). The anterior part has been destroyed and shows impressions of a number of internal features: *nsf*, canals of nerves of lateral sensory field; *rv*, rostral vein; *sof*, supra-oral field. Fig. 13. Counterpart of holotype (P.23011b) showing impression of external surface. Fig. 14. Outline restoration of cephalic shield.

as the supra-oral field, the aortic groove, the naso-hypophysial openings, canals of nerves of the lateral sensory fields, and of a rostral vein.

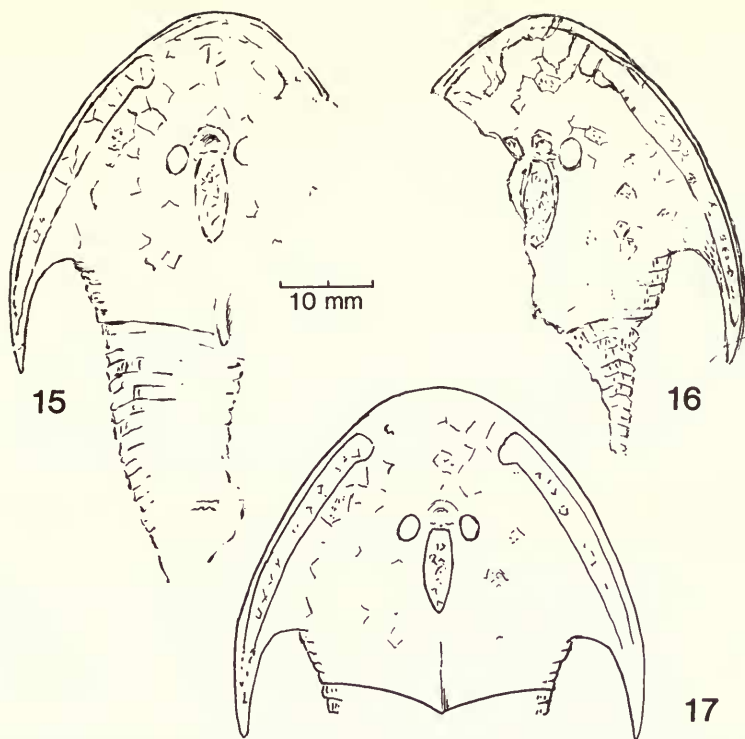
REMARKS. The only other species of *Cephalaspis* from the Anglo-Welsh area similar to *C. cwmmillensis* is *C. heightingtonensis* Stensiö (1932: 97; pl. 14, figs 5-7), but that species is even smaller and relatively broader, and among other obvious differences, the orbits are further forward, the cornua have denticles along the inner margins, and the pectoral sinuses are shallower.

Among the several species comprising small individuals from Spitsbergen described by Wängsjö (1952) none bears much resemblance to *C. cwmmillensis*, and the same remark applies to those from Scotland described by Stensiö in 1932.

***Cephalaspis abergavenniensis* sp. nov.**

Figs 11, 15-17

DIAGNOSIS. A small species of *Cephalaspis* with maximum breadth of headshield, at tips of cornua, about 1.25 times as great as length of shield in median line. Shield narrows rapidly and evenly forward without forming rostral angle but with sides in continuous curve with cornua, which are rather stout and of medium length, pointing almost directly backwards and reaching somewhat beyond level of interzonal median angle; inner side without denticles. Pectoral sinuses rather narrow and very deep. Interzonal part broad and long with very obtuse median posterior angle and clearly comprising at least five rows of body-scales, with low median crest projecting only slightly behind. Dorsal sensory field elongated oval in shape, three times as long as maximum breadth. Lateral sensory fields extending well onto cornua. Orbital openings situated well in front of middle of median length, about equidistant from centre of rostral margin and pectoral sinuses. Small independent pineal plate present. Circumnasal fossa large with



Figs 15–17 *Cephalaspis abergavenniensis* sp. nov. Fig. 15. Dorsal view of holotype (P.61034a). Fig. 16. External impression of counterpart of holotype (P.61034a). Fig. 17. Restoration of holotype.

prominent rim. Outer parts of exoskeleton of shield conspicuously subdivided into polygonal areas by circum-areal mucous grooves. Ornament of exoskeleton of shield of numerous small but well separated stellate tubercles, increasing slightly in size and becoming thorn-like towards back of shield and ridge-like on scales of body.

HOLOTYPE. An imperfect cephalic shield with much of the body attached, in counterpart, P.61034a, b: Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

DESCRIPTION. This small specimen is reasonably well preserved and was certainly complete when first collected, but now lacks the caudal half of the body and part of one side of the head-shield, and even more of the body in the counterpart. It lies on a slab with the remains of at least three specimens of *C. cradleyensis*.

The median length of the cephalic shield is 36 mm and the maximum breadth, flattened, is 44 mm across the middle of the cornua; the breadth of the interzonal part between the posterolateral angles was about 24 mm. The length of the cornu is 12 mm, and the distance of its tip from the centre of the rostral margin is about 44 mm. The distance of the pineal plate from the posterior angle of the shield is 20 mm and from the rostral margin 15 mm, so that the orbital openings are much nearer to the front of the shield: they are about 14 mm from the pectoral sinuses and are oval, measuring 3×2.5 mm.

A small independent pineal plate is present and the circumnasal fossa is large with a conspicuous rim.

The shield is rather broad at the level of the cornua, but it narrows fairly quickly towards the front without forming a rostral angle.

The interzonal part is 24 mm broad between the posterior lateral angles and is long, being clearly made up of five or six body-scales which are incompletely fused at the sides. There is a

short, low median ridge well separated from the median sensory field in front of it, which scarcely protrudes beyond the very obtuse posterior angle.

The median sensory field is elongate-oval in shape, measuring approximately 9×4 mm, and the lateral sensory fields are long and narrow, well separated in front, where there is a small expansion, and behind they pass for some distance onto the cornua.

The surface of the shield is divided into moderately-sized polygons by the mucous grooves which, as usual, are much smaller on the sensory fields.

The surface of the shield is ornamented with small but conspicuous stellate tubercles, which become somewhat larger and more thorn-like backwards towards the body and become short ridges on the squamation. There are impressions of parts of about 20 rows of scales to be seen.

REMARKS. Like the other diminutive single-specimen species associated with *C. cradleyensis* at Cwm Mill *C. abergavenniensis* is readily distinguished from any other species recorded from the Anglo-Welsh areas or from Spitsbergen, in this instance by its simple, rather wide cephalic shield, the 'craquelure' of the outer surface, the long interzonal part with its marked composite scale-structure and short, low median ridge, together with its very diminutive size.

Subgenus *CWMASPIS* nov.

DIAGNOSIS. Small species of *Cephalaspis* with very wide cephalic shield, almost semicircular, without rostral angle but with very short cornua not even reaching level of acute posterior angle of very brief and broad interzonal part with low, small median ridge. Pectoral sinuses very shallow with no denticles on inner side of cornua. Dorsal sensory field long and narrow, oval, pointed at rear; lateral sensory fields not extending onto cornua and widely separated in front. Orbital openings situated well in front of middle of median length of shield and considerably nearer to rostral margin than to pectoral sinuses.

TYPE SPECIES. *Cephalaspis billcrofti* sp. nov. (only species).

REMARKS. The great breadth and shortness of the whole shield and the interzonal part with the extreme brevity of the cornua readily distinguish this species from all others and give it a likeness superficially to some forms of *Benneviaspis*, but the shape of the sensory fields and the position of the orbits are those of a true species of *Cephalaspis*.

Cephalaspis (Cwmaspis) billcrofti sp. nov.

Figs 18–20

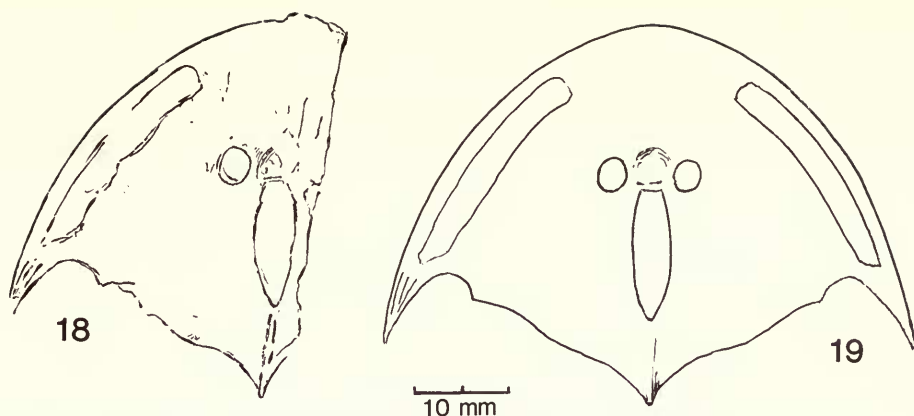
DIAGNOSIS. As for subgenus (only species).

HOLOTYPE. Imperfect head shield P.23012, Middle Dittonian, Cwm Mill, Abergavenny, Gwent. The only specimen.

DESCRIPTION. This small cephalic shield has lost nearly all the right side but there is sufficient remaining for the whole to be reconstructed (Fig. 19).

The shield is extremely wide and short and the surviving cornu is very short indeed, probably not exceeding 10 mm in length, without any denticles along the inner edge. The front margin of the shield forms a continuous curve from side to side with no suggestion of a rostral angle and the maximum breadth, across the tips of the cornua, was approximately 56 mm, and the median length only some 40 mm: even so, the point of the median posterior angle was some 7 mm behind the level of the tips of the cornua. The interzonal part of the shield was very short but broad, measuring about 40 mm between the posterolateral angles which lie far forward, so that the pectoral sinuses were very shallow and narrow, and the posterior border is somewhat sigmoidal between the posterolateral angles and the slightly projecting median point formed by a short and shallow median ridge.

The dorsal sensory field is 13 mm long, in shape an elongated oval, pointed behind, with a maximum breadth of about 4 mm. The lateral sensory field preserved is short and pointed



Figs 18–19 *Cephalaspis (Cwmaspis) billcrofti* subgen. et sp. nov. Fig. 18. Dorsal view of holotype (P.23012). Fig. 19. Restoration of holotype.



Fig. 20 *Cephalaspis (Cwmaspis) billcrofti* subgen. et sp. nov. Dorsal view of holotype (P.23012); $\times 2.1$.

behind; it does not reach onto the cornu. Anteriorly the lateral sensory fields must have been widely separated.

The orbital openings were situated well in front of the middle of the median length of the shield and measure approximately 4×3.5 mm.

A separate pineal plate is present, lying some 15 mm from the centre of the anterior margin and about 22 mm from the tip of the posterior angle of the interzonal part. The circumnasal fossa is conspicuous.

The exoskeleton has a fine granular surface.

REMARKS. There is no other species of *Cephalaspis* with which this form may be confused. It is named for W. N. (Bill) Croft who discovered this interesting section in the course of a comprehensive study of the Lower Old Red Sandstone of the area which unhappily he did not live to complete.

Summary of the fauna of the siltstone lenticle:

Cephalaspis cradleyensis Stensiö – About 40 specimens

Cephalaspis cwmillensis sp. nov. – One specimen

Cephalaspis abergavenniensis sp. nov. – One specimen

C. (Cwmaspis) bilcrofti subgen. et sp. nov. – One specimen.

The fauna of the 'Darker Bed'

The so-called 'Darker Bed', of which the siltstone lenticle presumably forms part, is to be found in Units 2 or 3 of the cyclothem at Abergavenny described by Allen (1964: 184–7, fig. 11). The fauna is not only different from that of the lenticle but very differently preserved: instead of being crowded together, flattened and comprising complete animals, the fossils are well separated, three-dimensional and broken usually into fairly large pieces, and bodies (with one exception) and tails are completely absent. *Cephalaspis cradleyensis* is present but rare in the material collected (Fig. 2), but dorsal and ventral discs of young or a small form of *Pteraspis* (*Belgicaspis*) *crouchi* are common, as are plant fragments. There are also three substantial pieces of a much larger species of *Cephalaspis* than *C. cradleyensis*, and of these two may well be parts of the same cephalic shield (P.22995–7). One specimen shows a round orbital opening about 5 mm in diameter and lanceolate dorsal sensory field 14 mm long with a maximum breadth of 3.5 mm; the other specimen has a low but distinct dorsal crest on the interzonal part; in both the outer surface is smooth.

The third piece has a short but powerful cornu 22 mm long directed slightly outwards, a rather narrow pectoral sinus and part of a narrow lateral sensory field running onto the cornu.

There is yet another specimen from the 'Darker Bed' that is worth a mention for, although very imperfect, it is clearly different from any of the other specimens recorded from the locality and part of the body is preserved in impression. The matrix is different; although dark it has red rustlike markings and is very sandy, so that the specimen (P.60872) is extremely fragile. It shows the impression in counterpart of the ventral surface of the left cornu and the left side of the body as far as the base of the tail, and there is a faint outline of perhaps three-quarters of the cephalic shield. The total length of the animal preserved was approximately 65 mm, while the maximum breadth of the shield at the level of the tip of the cornu is estimated at 44 mm. The cornu itself at 15 mm is relatively long and there is no sign of denticles along the inner margin. It is 4 mm broad at its base. The pectoral sinus is deep and rather narrow. The outlines of the small ventral scales are in places well shown with fine horizontal ridges. There are just enough characters to make it clear that it does not belong to the same species as any of the other specimens of *Cephalaspis* from Cwm Mill but insufficient to carry identification further. Much the same may be said of the three larger fragments from the 'Darker Bed' already described, and they cannot be positively associated with any of the congeners from the type-locality of *C. cradleyensis* (Stensiö 1932: 200).

The occurrence of specimens of *Cephalaspis*

The wide range in time and space of the cephalaspids (Wängsjö 1952: 9–14; Halstead & Turner 1973: 74, figs 7–9), in particular of the type genus *Cephalaspis* Agassiz (*sensu lato*), at one time promised to provide a valuable means of correlating and dating the strata of the Lower Old Red Sandstone in its several apparently discrete areas. But as Wängsjö rather sadly remarks in his admirable monograph on the cephalaspids of Spitsbergen (1952: 585), 'for a safe correlation

with other areas . . . the Spitsbergen Cephalaspids are in general of fairly little importance . . . as the species apparently were not very widespread'. Only two forms, *C. cradleyensis*, then a very rare species from the Anglo-Welsh Borders, and a new variety of the Scottish *C. powriei*, each represented in Spitsbergen by a single very imperfect cephalic shield, provide tenuous links with other areas. Further, we may note that no species as yet has been recorded as common to the neighbouring Scottish and Anglo-Welsh areas.

Worthwhile specimens of *Cephalaspis* are not so very common considering the very large regions and the thickness of Lower Devonian non-marine strata from which specimens have been collected for many years. The Spitsbergen material, on which Stensiö (1927: v–ix) based his classic anatomical studies, dates from collections made from 1909 to 1926, but these specimens and those collected in 1939 on which Wängsjö based his researches (1952) were much less satisfactory from the purely systematic point of view, and thus for precise correlation, owing to natural imperfection of the specimens and so to the relative scarcity of those that could be clearly named specifically. Wängsjö could identify satisfactorily only about 160 specimens of the genus from the combined Red Bay and Wood Bay formations, while more than 20 species were based on single imperfect cephalic shields. As Wängsjö himself remarked (1952: 249), 'In such cases the diagnosis is, of course, only preliminary', a comment that is unhappily of almost universal application.

The specimens from the Midland Valley of Scotland are very different in their state of preservation, especially in Angus (Tayside) in the north-eastern part, where numerous nearly complete animals have been found (Stensiö 1932: pls 25, 28, 30–40, 43, 46). In some quarries they are flattened, but in others the shape of head and body has been well maintained, as with the lectotype of *Cephalaspis lyelli* Agassiz (White 1958a), and isolated cephalic shields also occur uncrushed.

The specimens of *Cephalaspis* so far described from the Anglo-Welsh Borders resemble those of Spitsbergen in consisting almost entirely of isolated cephalic shields: indeed, out of a total of about 65 specimens recorded by Stensiö (1932) only three had part of the body attached. Although on the whole much better preserved in regard to external features they show very little indeed of the internal anatomy.

The first specimens of *Cephalaspis* were described by Agassiz (1835), yet after nearly a century Stensiö (1932), in his comprehensive monograph of the cephalaspids of Great Britain, could muster no more than 141 worthwhile specimens for the record, 77 from Scotland and 64 from England. Doubtless other specimens were unaccounted for, simply because they were unknown or not available to the author at the time the monograph was written, but even so the numbers are strikingly small. In the Anglo-Welsh area the relative scarcity of specimens is in great measure due to the high degree of cultivation of the land and its generally flat topography. Moreover, the Lower Old Red Sandstone there is in general too soft to occasion large-scale quarrying for building material. Indeed, until fairly recent times much of the collecting seems to have been done rather casually by amateurs, largely from the labourers in small temporary pits opened up for farming or other local purposes. This does perhaps explain the all too frequently poor condition of the specimens and also the very common separation or loss of valuable counterparts, with the consequent loss of important information in the description of rare species: one may note that of the twenty-three species and varieties of the genus *Cephalaspis* described from Great Britain by Stensiö fifteen type specimens have no known counterparts to date. Four have counterparts shared by different institutions, and of the other four species now with counterparts three had the two sides, or parts thereof, reunited after many years of separation. The lectotype of *C. lyelli* Agassiz was reunited after 36 years (20087, presented by Sir Charles Lyell in 1846; P.3233, in the Enniskillen collection 1882); the holotype of *C. lankesteri* after 58 years (45943 in the Lightbody bequest 1874; P.16155 originally in the Hereford Museum and presented to the BM(NH) in 1932); and the holotype of *C. cradleyensis* after 47 years (P.5375, H. B. Hill collection 1887; P. 16960, Bootle Museum presentation 1934 – as related above, p. 152). The only instance of a holotype and its counterpart being kept together in all the Scottish and Anglo-Welsh material described by Stensiö is that of the little cephalic shield of *C. heightingtonensis* which was purchased complete in 1864.

The growth and distribution of *Cephalaspis*

Questions relating to the individual growth, original source and dispersal of the Agnatha in general have long been matters of discussion. As regards the cephalaspids and the genus *Cephalaspis* in particular, it has long been noticed that no juvenile stages have ever been recorded, and Westoll (1945, 1946, 1958: 192), Denison (1947, 1951, 1956) and White (1958*b*) on this and other grounds came to the not unreasonable conclusion that 'at least many cephalaspids acquired their bony skeleton only when fully grown'. That this was so seems now to be generally accepted (Wängsjö 1952: 247). Such a late development of the armour fits in very well, as an adult character, with the idea that the earlier Osteostraci were entirely soft-bodied, which in turn does away with a major objection to the theory that the Agnatha were marine or at least coastal in origin by explaining the absence of their remains in salt-water deposits. Such an environment would readily explain their very wide and relatively swift distribution. Even so, it is still rather difficult to explain the complete absence of partly grown specimens, rapid though the development of hard parts may have been. Clearly it is a matter of habitat and where such a metamorphosis could have taken place – obviously not in the area of formation of the usual Lower Old Red facies. There is in fact just one specimen in the collection from Cwm Mill that seems to show incompletely formed hard parts. This specimen (P.23005a, b; Fig. 4, p. 154) is slightly smaller than average specimens of *C. cradleyensis* and is worth special consideration. It is a whole animal with tail and is on the same surface of rock as a normally-developed example of *C. cradleyensis*. Like that specimen, it is completely flat and in counterpart, yet only the outlines of its various features can be seen: it is just a ghost of a specimen. It cannot have been dissolved away after entombment, for nothing has affected the adjacent specimen, which is perfectly normal in its condition: it does suggest very strongly a young animal in the early stages of forming its armour. If this interpretation of the fossil is correct it indicates that ossification took place evenly more or less throughout the animal.

From the acquisition of the hard parts at full growth stage and the subsequent inability to expand further, it follows that all specimens of a species should be roughly of the same size. Therefore size was a specific character, and this seems to have been tacitly understood in the composition of specific diagnoses. Wängsjö (1952: 247), in writing on the Spitsbergen forms, remarks that 'the shields preserved are always from full grown individuals . . . the variation on the length of the shield in a single species seems to be at most about 20% of the mean length.' However, the range in size of some of the British species as described by Stensiö (1932) seems to have been much greater than was anticipated: that is, if the identifications are accepted as correct.

The following are the variations in the median length of the cephalic shield in five forms, with percentage variation:

<i>C. salweyi</i>	80 to 145 mm in 14 specimens	80% variation.
<i>C. whitei</i>	45 to 70 mm in 21 specimens	65% variation.
<i>C. pagei</i>	20 to 60 mm in 32 specimens	200% variation.
<i>C. powriei brevicornis</i>	51 to 78 mm in 8 specimens	53% variation.
<i>C. powriei asper</i>	60 to 80 mm in 6 specimens	33% variation.

The first three species certainly call for further consideration and answers may lie between preservation and identification: certainly more than one species is covered by *C. whitei* as originally described.

Other general questions relating to the species of the genus concern the actual habitat and the proliferation of species at the same level and locality.

The later Dittonian deposits, in which the remains have been found most abundantly in the Anglo-Welsh region, have been admirably documented and discussed (e.g. Allen & Tarlo 1963: 398, Allen 1964: 194, Allen 1979): we may note that 'the Dittonian facies of the Welsh Borderland has been interpreted as the deposit of a floodplain complex' and comparison made with the modern sediments of the Colorado Delta and River (Allen 1963: 398). The climate was

'probably warm to hot' (Allen 1974: 152), at any rate in the not so distant Clee area, and that according to authors there quoted southern Britain was on 'the borders of a major arid zone' or 'in the southern hemisphere within a few degrees of latitude of the Devonian palaeomagnetic equator'.

However, there are one or two important points that invite further comment. Allen & Tarlo (1963: 144-6) state that 'During early Dittonian times . . . the vertebrates must all have been freshwater living' and 'in the main have been transported downstream after death', and again in the Ditton Group that 'Although the vertebrates show evidence of water sorting and transportation after death, and some were clearly reworked through the floodplain, there can be no doubt that as in the "*Psammosteus*" Limestones Group, the animals inhabited the fresh waters of rivers.' Lastly, Allen (1979: 67) remarks that in his distal alluvial facies 'The vertebrates emerge as channel-dwellers for at least part of their lives, their remains tending to accumulate, after much reworking, in the lag deposits formed on the channel floors.'

It is undoubtedly true that the cephalaspids were inhabitants of fresh waters, not of the rivers in the floodplains to which their disintegrated remains were commonly carried by stream action, but as inhabitants of the upper reaches, the head waters, lakes and the like, from which sometimes the complete animals were swept by storm action, generally dead and decaying but occasionally still alive and subsequently dying when the resultant pools dried up. The floodplains and the annectent rivers and channels were not the natural environment of the cephalaspids, they were their mortuaries and graveyards. The statement (Allen & Tarlo 1963: 146) that 'The majority of the cephalaspids were obviously able to survive considerably longer [than the pteraspids and a few cephalaspids] in such an unfavourable environment' as had existed at the time of the Cwm Mill or of any other deposition must be considered a misinterpretation of the facts.

The species of *Cephalaspis* were evidently poor swimmers. Their forelimbs were not primarily paddles to aid in progression but balancers to check the depressing effect of the relatively large and somewhat incongruous heterocercal tail, virtually the only means of propulsion, and of the heavy armoured head.² Active animals would not require so complete a protection as in these creatures, and the flattened undersides of both head and body as well as the form of the transverse mouth clearly proclaim them as bottom-living scavengers largely suctorial in their feeding; as such they would not fare very well in the intermittent torrents and rivers of the floodplains. The idea of carriage from a considerable distance is clearly supported by the rarity of the preservation of the body or its elements, so manifest in the Spitsbergen and Anglo-Welsh provinces.

Comment has already been made on the way in which cephalaspids, along with other Agnatha, 'generally appear at particular horizons only, and are replaced by entirely different forms' (Allen & Tarlo 1963: 151). This indeed may be so, but the evidence so far published in regard to the systematics of the cephalaspids and to the relative levels of the known localities leaves much to be desired, especially in the two provinces in Great Britain. The further remark that 'This individuality can best be explained by postulating a series of immigrations to the Anglo-Welsh Province, . . . as the presence of some of the genera and species in such distant Provinces as Podolia and Spitzbergen can only be accounted for by a faunal interchange via the sea' conjures up the interesting but unlikely picture of endless waves of naked young cephalaspids, constantly differing in species, largely local in origin but with an occasional

²The suggestion of Janvier (1978: 22) that 'ces nageoires étaient capables de mouvements latéro-mésiaux importants' on the evidence of supposedly special smooth areas on the dorsal and ventral surfaces of the cornua 'chez presque tout les Céphalaspidiés' is certainly not acceptable as a general rule, at least for the earlier, more typical species of the genus *Cephalaspis* (s.l.), for of the twenty species recorded from Great Britain by Stensiö (1932) no less than eleven bear spines or denticles along the inner margins of their cornua, and of these eight are described as having also narrow pectoral sinuses, a combination that would have made the movement of fins up and down past the level of the cornua impossible without damage. From the Red Bay Series of Spitsbergen out of thirty-seven recorded species nine had the double handicap of denticles and narrow sinuses, but in the succeeding Wood Bay Series in only one species are such denticles said to have been present. That species had a very wide head-shield with very wide pectoral sinuses, like most of the other species known from the formation, a trend that certainly would have allowed freedom of movement to the pectoral fins.

intruder from foreign parts, assembling in estuaries from time to time over millions of years, waiting to don their armour prior to facing the dangers of fluvial ascent. Further, the notion that these seemingly sluggish bottom-feeders should have in any way anticipated the life-wanderings of either salmon or eel seems an even nearer approach to the realms of fantasy.

Wängsjö (1952: 570–1) gives a good generalized idea of the coming-in and disappearance of cephalaspids and doubtless provides a pattern for the occurrence of the genus *Cephalaspis* in other provinces, that is, of the intermittent appearance of apparently unrelated species, often several at a time but differing in number and very restricted in time and usually in area, but generically covering a very great period of time and thickness of strata. The injection of fresh species at irregular intervals is not acceptable if it is agreed that the cephalaspids were originally soft-bodied and marine in habitat and only developed hard parts when fully grown and established in fresh water. An endless succession of such metamorphoses taking place over the millions of years that the genus spanned seems less than likely, nor is the development of almost endless congeneric species in the open sea a probability.

If, on the other hand, *Cephalaspis* was first established in fresh waters, it was likely to have been much more active in its original unarmoured condition than in its ultimate adult development, allowing the animals to ascend the rivers to the quieter permanent headwaters in the 'distant land masses' in the north of 'Euramerica' (Young 1981: 226, fig. 1). These waters were possibly in the form of large connected lakes or inland seas, rather after the pattern of those in central Africa (White 1950: 58), and may have been sufficiently extensive to cover the drainage systems of all the Cephalaspid Province. At this stage adult armour was presumably developed against newly-encountered earlier resident predators, such as eurypterids and large acanthodians (Miles 1973), and subsequent diversification must have taken place in these relatively quiet waters after the manner of the living cichlid fishes in Africa (Greenwood 1974). It is interesting to note that Greenwood (1974: 112) records that in Lake Victoria 'over 150 species [of the genus *Haplochromis*] have evolved within little more than three-quarters of a million years, from one or at most a few closely related species', and that in the smaller Lake Nabugabo five endemic species of the same genus have evolved since the lake 'was isolated from Lake Victoria by a sand spit formed some 3500 years B.P.' The analogy cannot, of course, be taken too far, since one is dealing with different animals, and at vastly different periods of time, and there is one major factor in the speciation of the cichlids that the cephalaspids lack, and that is variation in dentition and hence in diet. Heintz (1940: 181–2) has indeed indicated some differences in the external details of the oral area in some cephalaspids but there is no indication of change in their microphagous diet.

If the major habitat of the cephalaspids was, as has been suggested, in the fresh waters of the distant uplands, it would explain the spasmodic appearance of their remains in the floodplain deposits, as the results of overflow following unusual rainfall in the region of the headwaters. The generally disarticulated condition of the fossils resulting, with very rare exceptions, in nothing but isolated cephalic shields, was due to the distance corpses were carried and the time that it took, and the readiness with which the flimsy, lightly attached scales would be dispersed and carried away once decay had set in.

That very occasionally there should occur very local, usually lenticular deposits in which complete animals with the bodies and fins intact are to be found, as at Cwm Mill and Wayne Herbert, is to be expected as a result of the floodwaters from exceptionally violent storms in the uplands rapidly carrying still living or moribund animals down the rivers to be immediately entombed in the drying-up pools of the warm floodplains. That the lenticle in the somewhat younger section at Wayne Herbert should have yielded a much more widely diversified fauna than at Cwm Mill is merely a reflection of the local circumstances at the time.

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